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CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE, E. L. MARK, DIRECTOR, No. LXXIII.

STUDIES IN MORPHOGENESIS, VI.

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Presented October 14, 1896.

The following quantitative study of variation is based upon counts of the Müllerian glands of the fore legs of 4,000 swine. Our attention was directed to these glands as favorable objects of study by Gertrude Crotty Davenport, who had already collected some data concerning their variability. These data, together with valuable suggestions derived from her own experience, she generously placed at our disposal.

The positions of the Müllerian glands are indicated upon the wrist by large openings or pits, about 1 mm. in diameter, which are found only upon the inner aspect of the fore legs. The number of pits is variable. Where there are several they occur, for the most part, in a single row trending somewhat obliquely to the long axis of the leg.

Of the 8,000 legs examined, the arrangement of the glands was studied on only 2,000 legs, 1,000 male and 1,000 female. The total number of glands on a single leg varies from 0 to 10. When the number is large, some of the glands are frequently found outside the main row. In no case have we found more than nine glands in one row. We may call those lying outside the main row *lateral* glands. The lateral glands usually (six exceptions) occur at the upper (proximal) end of the series. Their number does not usually exceed two, but in a single case we have found four. These four glands lay in a secondary row parallel to the main row, which contained five glands. In one other case, where three lateral glands were found, these lay parallel to the main row of five. When there are two glands they may lie either in a line parallel with the main row, or make any angle up to 90° with it. Lateral glands occur more rarely when the total number of glands on the leg is small, but we have found one extreme case in which the only two glands on the leg occurred side by side, i. e. in a transverse row.

The reduction in the number of glands takes place from one end, — the distal end of the series. Generally, where there are only two or three glands these occur high up and the normal diatance apart. Rarely, however, the reduction is brought about in part by the failure to develop in the middle of the series while glands develop near the extremes, so that there is a broad hiatus in the series.

Since the proximal end of the series is that at which glands are most likely to be formed, and since they tend to be produced more abundantly there, this end, which occupies the region of the upper wrist, is to be considered as the source of the morphogenic impulses which give rise to the glands. Sometimes the embryonic Anlage does not develop beyond this point; sometimes, on the other hand, it develops along the whole extent of the wrist in one row, and even forms an accessory "lateral" row.

The total number of swine examined was, as stated, 4,000; of which 2,000 were males and 2,000 females. The total number of fore legs examined was, accordingly, 8,000; 4,000 left and 4,000 right. All of the observations fall, consequently, into four groups of 2,000 cases each; namely, male right, male left, female right, female left. These four groups will be considered, for the most part, separately.

We first determined how many legs in each of these classes had no glands, one gland, two glands, and so on. The results are given in the following table.

TABLE I.

No. of Glands.	0	1	2	3	4	5	6	7	8	9	10	Total.
♂ R	15	225	353	437	411	297	155	78	16	12	1	2,000
♂ L	14	241	336	430	429	295	159	53	30	10	3	2,000
Total ♂	29	466	689	867	840	592	314	131	46	22	4	4,000
♀ R	15	209	365	482	414	277	134	72	22	8	2	2,000
♀ L	21	213	361	438	432	288	149	69	16	11	2	2,000
Total ♀	36	422	726	920	846	565	283	141	38	19	4	4,000
Total ♂ + ♀	65	888	1415	1787	1686	1157	597	272	84	41	8	8,000

In the following table, which is based upon the preceding, the numbers are all reduced to per milles. The two lines of totals are here, accordingly, replaced by means. A glance at this table shows a close parallelism between the distribution of glands in the four cases.

TABLE II.

SUMMARY PER MILLE.

No. of Glands.	0	1	2	3	4	5	6	7	8	9	10
♂ R	7.5	112.5	176.5	218.5	205.5	148.5	77.5	39.0	8.0	6.0	0.5
♂ L	7.0	120.5	168.0	215.0	214.5	147.5	79.5	26.5	15.0	5.0	1.5
Mean ♂	7.2	116.5	172.2	216.8	210.0	148.0	78.5	32.8	11.5	5.5	1.0
♀ R	7.5	104.5	182.5	241.0	207.0	138.5	67.0	36.0	11.0	4.0	1.0
♀ L	10.5	106.5	180.5	219.0	216.0	144.0	74.5	34.5	8.0	5.5	1.0
Mean ♀	9.0	105.5	181.5	230.0	211.5	141.3	70.7	35.2	9.5	4.7	1.0
Mean of ♂ and ♀	8.1	111.0	176.8	223.4	210.7	144.7	74.6	34.0	10.5	5.1	1.0

Several interesting questions now arise:

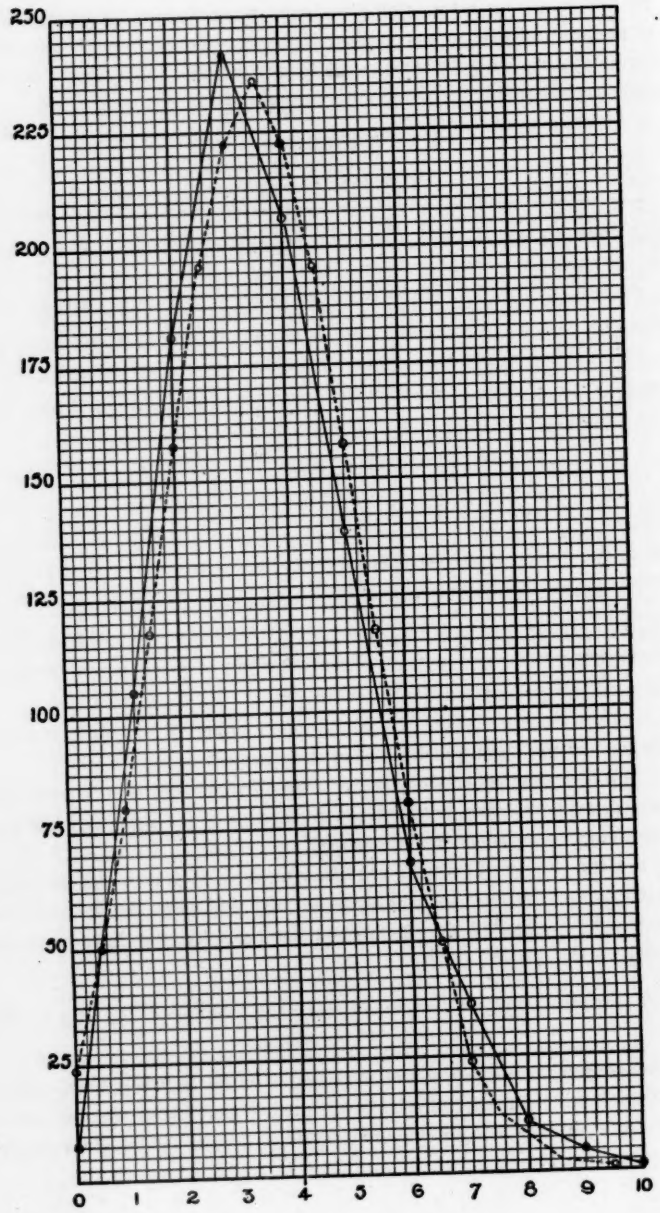
(1) How closely similar is the average number of glands in the two sexes, and in the right and left leg of the same sex?

(2) Which sex shows the greater variability, and to what extent is it greater? Is the relation between the variability of the right and left legs closer than that between the two sexes?

(3) How closely correlated are the numbers of glands on the right and left legs of individuals? That is to say, what are the chances that a swine which has 2, 4, or 7 glands on the right leg will have the same number on the left leg also?

1. *The Relation between the Abundance of Glands and the Sex or the Side of the Body.*

The average number of glands on a leg of either sex is determined by dividing the total number of glands counted in that leg by the number of individuals of that sex, in this investigation 2,000. This gives us the following result: —


250
225
200
175
150
125
100
75
50
25
0
1
2
3
4
5
6
7
8
9
10

1.	Average number of glands in			♂ R	3.547
2.	"	"	"	♂ L	3.540
3.	"	"	"	♀ R	3.501
4.	"	"	"	♀ L	3.521

Comparing the average of (1) and (2) with the average of (3) and (4) it appears that the average number of glands in the males (3.544) is tolerably close to that in the females (3.511) but that a real difference exists between the two. *The glands are slightly less abundant in the female than in the male in the ratio,* 100 : 100.94. The average number of glands on the right side of the body is so close to that on the left side (3.524 : 3.531) that we may conclude: *The average numbers of the glands on the right leg and on the left leg taken without regard to sex are about equal.*

2. *Variability correlated with the Sex and with the Side of the Body.*

In seeking to determine whether, in this matter of glands, male or female swine are the more variable, it is necessary to employ a method of stating variability quantitatively. Quetelet, Stieda, and Galton* have employed such a method, based upon the fact that the organs of an animal vary about their mean dimensions to an extent and with a frequency indicated by the probability-of-error equation,†

$$y = k \cdot e^{-h^2x^2}.$$

Two of the principal features involved in such a distribution are that deviations of a given size are equally apt to occur above and below the mean, and that small deviations are more apt to occur than large ones. These and other characters of the "probability" curve are indicated in that shown in dotted line in the accompanying diagram. The diagram also shows the curve of distribution of the various numbers of glands occurring on a leg, from 1 to 10. This curve is drawn from the right female leg only; the curve for the other legs would be very similar. We shall speak in a moment of the method of construction of these curves; but we want now to call attention to the fairly close similarity of the two curves, — that gained by observation and the theoretical one, — a similarity so close that we are justified in concluding that the law of distribution of the variants in the leg glands of swine is the same as that of accidental errors.

* Quetelet, Lettres sur la théorie des probabilités, Bruxelles, 1846. Stieda, in Archiv für Anthropologie, Bd. XIV. pp. 167–182. Galton, Natural Inheritance, New York and London, 1889.

† See any text-book on "Least Squares."

This being granted, we can express quantitatively the degree of variation in the glands by determining the *average deviation* in the number of glands of any set of legs from the mean number of that set. Thus in the right leg of the female the mean number of glands is approximately 3.5. Since there is no individual with 3.5 glands on the leg, every individual shows in the number of its leg glands a departure of at least 0.5 from the mean. Adding together the departures of every individual and dividing by the total number of individuals (2,000) we get the mean departure, which is known to mathematicians as the mean error, and is indicated by the formula $\frac{\Sigma x}{n}$, in which Σx indicates the *sum* of the individual departures, x, and n the total number of individuals. Proceeding in this way, the average departure, as an *Index of Variability*, was determined to be as follows for each set of legs: —

Average departure	of	♂	R	1.41089
"	"	♂	L	1.41083
"	"	♀	R	1.36457
"	"	♀	L	1.38766

These determinations indicate that the variability of the right and the left legs, of the male is exactly the same to four places of decimals; that the variability of the right leg of the female is slightly less than that of the left leg, and that the male shows a greater variability than the female in the ratio of about 1.411 : 1.376, or 1.025 : 1.000. In other words, the male is 2.5% more variable than the female.

As we have seen, the variabilities of the right and of the left sides of the male are practically equal. In the female, the left side is more variable. Disregarding sex, we find the variability of the left side is to that of the right as 1.3993 : 1.3877, or as 1.0084 : 1. That is to say, the glands are 0.8% more variable on the left side than on the right.

Let us now compare the relative variability of symmetrical legs with that of the two sexes. We find the variability to be greater between the same leg (say the right) in opposite sexes, than between symmetrical legs. The relation may be expressed by the ratio 1.025 : 1.0084, or 1.016 : 1. These numbers indicate a closer morphogenetic kinship between the two legs of a symmetrical pair than between the corresponding leg in different sexes.

We may now briefly indicate the method of constructing the probability curve in the diagram. The abscissas represent the numbers of glands from 0 to 10 on a leg, and the ordinates the corresponding number

of individuals per mille. The mean number of glands is 3.50 and the index of variability is 1.3646. With these data, we can draw a probability curve including about the same area as our observed curve. This curve, the continuous line, is drawn from the equation

$$y = k \cdot e^{-h^2 x^2}.$$

h is the so called index of precision, and is equal to the reciprocal of the index of variability divided by the square root of π, thus,

$$h = \frac{n}{\Sigma x \sqrt{\pi}}.$$

e is the base of the Napierian system of logarithms; namely, 2.1718.

k is a constant determined by multiplying the quotient of $\frac{h}{\sqrt{\pi}}$ by the interval (dx) between successive values of x, in this case, 1; thus,

$$k = \frac{h\,dx}{\sqrt{\pi}}.$$

x indicates deviations from the mean value, and y the corresponding ordinates.

When $x = 0$, $y = k$, which is thus the length of the ordinate at the mean value of x. Its value gives the percentage of cases which should theoretically occur at the mean; it is in this case 23.3%. Like h, k might be taken as a measure of precision, since it increases as variability diminishes.

3. *The Degree of Correlation between the Number of Glands on the Right and the Left Legs of Individuals.*

To get quantitative results in this matter we must employ a method devised by Galton.* This method depends upon the following procedure and considerations. Separate the right legs into as many lots as there are degrees of deviation from the mean number of glands. These lots may be called the subjects. Find for each of the subjects the mean deviation in the number of glands on the left legs of the corresponding individuals (the relative). The deviation of any subject and the deviation of the corresponding relative are to be compared. In order to make this comparison instructive, we must take into account the fact that left legs (for example) are more variable than right legs. In order to eliminate this

* Galton's method is explained in his paper in the Proc. Roy. Soc., Vol. XLV. p. 135, 1889.

difference, divide the deviation of the subjects by their index of variability and the deviation of the corresponding relatives by their index of variability. If now, the correlation is perfect, those causes which have produced a deviation from the mean in the right leg will act in precisely the same degree on the left leg also, and thus the deviation of any relative will not differ from the deviation of the corresponding subject. If, under these circumstances, we divide the mean deviation of the relatives by that of the subjects, the quotients will average 1. This average quotient is called the Index of Correlation. Thus, the index of perfect correlation is 1.

Let us suppose, on the contrary, that there is no correlation whatever between the number of glands in any subject and in the corresponding relative, then, no matter what the number of glands in any subject, the number in the corresponding relative is just as apt to be large as small, and will be equal to the average number of glands in the whole group; in other words, no matter what the deviation of the subject is, that of the relative will be 0. The average quotient obtained, under these circumstances, by dividing the deviation of relatives by the deviation of the subjects, will consequently always be 0. Thus the index of entire lack of correlation is 0.

An inverse correlation, in which a positive deviation of the subject from the mean shall always be accompanied by a negative deviation of the relative, will be represented by a minus quantity. Thus the correlation of any two sets of compared organs will lie between $+1$ and -1. The size of the fractions lying between ± 1 and 0 will serve to indicate the degree of correlation.

The quotient, r, obtained by dividing the deviation (always in units of the average deviation) of the left legs by that of the corresponding right will not be the same for all the lots of individuals. The true index of correlation, R, will be found by taking the average of all the ratios, r, r', r'', r''', etc. This process of finding R may be somewhat abbreviated from the following considerations. We have seen that

$$r = \frac{\dfrac{\text{Deviat. of Rel.}}{\text{Avg. Dept. of Rel.}}}{\dfrac{\text{Deviat. of Subj.}}{\text{Avg. Dept. of Subj.}}} = \frac{\dfrac{d_r}{A_r}}{\dfrac{d_s}{A_s}};$$

also that

$$R = \frac{1}{n}(r + r' + r'' + \ldots . r^n) = \frac{1}{n}\Sigma r;$$

consequently,

$$R = \frac{1}{n}\left(\frac{\frac{d_r}{A_r}}{\frac{d_s}{A_s}} + \frac{\frac{d'_r}{A_r}}{\frac{d'_s}{A_s}} + \frac{\frac{d''_r}{A_r}}{\frac{d''_s}{A_s}} + \cdots \frac{\frac{d^n_r}{A_r}}{\frac{d^n_s}{A_s}}\right) = \frac{1}{n}\Sigma\frac{\frac{d_r}{A_r}}{\frac{d_s}{A_s}} = \frac{A_s}{A_r}\cdot\frac{1}{n}\cdot\Sigma\frac{d_r}{d_s},$$

since A_s and A_r are constant. It results from this that it is only necessary to find the mean of the ratios of the untransmuted deviations and multiply this by the quotient $\frac{A_s}{A_r}$. This saves a great many divisions, and it has been the method pursued in our work.

After this statement of the method of expressing correlation we now pass to a consideration of the results obtained with the glands of the pig. We shall consider first the correlation between the number of glands on the right leg of the male with that on the left leg of the male.

TABLE III.

♂ R CORRELATED WITH ♂ L.

Relatives. Subjects.	0*l*	1*l*	2*l*	3*l*	4*l*	5*l*	6*l*	7*l*	8*l*	9*l*	10*l*	No. of Indivs. Right leg.	Means of Lefts.	Dev. of Rel. (d_r)	Dev. of Sub. (d_s)	$\frac{d_r}{d_s}$ Quo.
0*r*	8	5	2	—	—	—	—	—	—	—	—	15	0.600	−2.940	−3.547	.829
1*r*	4	151	58	9	3	—	—	—	—	—	—	225	1.360	−2.180	−2.547	.856
2*r*	2	65	154	96	28	7	1	—	—	—	—	353	2.306	−1.234	−1 547	.798
3*r*	—	14	88	173	128	28	6	—	—	—	—	437	3.197	−0.343	−0.547	.627
4*r*	—	5	27	119	153	77	26	3	1	—	—	411	3.888	+0.348	+0.453	.768
5*r*	—	1	7	24	92	101	52	11	9	—	—	297	4.784	+1.244	+1.453	.856
6*r*	—	—	—	8	16	58	48	16	7	0	2	155	5.510	+1.970	+2.453	.803
7*r*	—	—	—	1	8	20	18	17	9	5	—	78	6.141	+2.601	+3.453	.753
8*r*	—	—	—	—	1	3	5	3	2	2	—	16	6.500	+2.960	+4.453	.665
9*r*	—	—	—	—	—	1	3	3	2	2	1	12	7.333	+3.793	+5.453	.696
10*r*	—	—	—	—	—	—	—	—	—	1	—	1	9.000	+5.460	+6.453	.846
No. of Indivs. Left Leg.	14	241	336	430	429	295	159	53	30	10	3	2,000		Mean,		.772

In this table the first column names the subjects, of which there are as many as there are numbers of glands, viz. 0 to 10. In the succeeding columns on a single line is exhibited the distribution of the number of glands on the corresponding left legs. The column headed "Means of Lefts" gives the average number of glands on the left legs of the individuals which make up the corresponding subject. The column headed "Deviation of Rel. (d_r)" gives the deviations of the corresponding "Means of Lefts" from the mean number of left male glands. The column "Dev. of Subject (d_s)" gives the deviation of the subjects from their mean number. The last column is the quotient of d_r divided by d_s. This gives r, r', r'', etc. The last number in the column is the mean of all these values of r. This number multiplied by $\frac{A_s}{A_r}$ will give R, the value sought. But $\frac{A_s}{A_r}\left(=\frac{1.41083}{1.41089}\right)$ is nearly unity, so that the Index of Correlation of the number of glands of the right and left legs is .772. Galton has shown that the same ratio holds true when relative and subject are interchanged.

By a process similar to the preceding we have found that the ratio of correlation of right and left legs in the female is .783. This ratio is so similar to that obtained for males as to justify the conclusion that *the index of correlation in variability of the leg glands is approximately equal in the two sexes, and is about .777.*

The conclusions from this study may now be summed up. We have in the leg glands of swine a serially arranged system of organs developing, for the most part, in one line, starting at one point, and extending out a variable distance. On such a system of organs we investigate quantitatively the question, How closely similar are the morphogenic processes which determine the resemblance of these glands on the opposite sides of the body and in the two sexes? First of all, the *average* number of glands is tolerably but not strikingly close on the two fore legs and in the two sexes. The glands are nearly 1% more abundant in the male than in the female. When we come to study their variability we find that the variants are distributed in accordance with the probability curve, very nearly. (See diagram.) A curious lack of symmetry results from the fact that, since the mean lies at 3.5, variation is limited to 3.5 in one direction, but is unlimited (reaches as a matter of fact to 6.5) in the other. The degree of variability in the right and left legs is, especially in the case of the male, strikingly similar, being 1.41089 and 1.41083 in the two cases respectively, the difference being within the

errors of the method. The males are about 2.5% more variable than the females. The glands are 0.8% more variable on the left side than on the right. The relative variability of the same leg in the different sexes is about 1.6% greater than that of the two legs in the same sex. The degree of correlation in the variability of the right and left legs is about .777.

CAMBRIDGE, MASS., July 25, 1896.